THE MORPHOLOGY OF COELOIDES DENDROCTONI CUSHMAN (HYMENOPTERA: BRACONIDÆ)

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Introduction

There can be little doubt that during the last forty years the barkbeetles of the genus *Dendroctonus* have killed, in the United States, more trees beyond the sapling size, and destroyed a greater volume of timber than any other insects. Craighead and Middleton (1930) state that several species of this genus annually destroy 6,000,000,000 board feet of timber valued from $15,000,000 to $20,000,000. The mountain pine beetle (*Dendroctonus monticolae* Hopkins) has been increasing at a rapid rate during the past 10 years in the National Forests of western Montana, Idaho, and eastern Washington. On the Coeur d'Alene National Forest in Idaho, from 1929 to 1932, a total of more than $236,000 was spent on control operations to destroy this beetle in the stands of western white pine (*Pinus monticola* Doug.). On the Beaverhead National Forest in western Montana about $150,000 was spent from 1927 to 1929 combating the same beetle attacking lodgepole pine (*Pinus contorta* Loud.). The number of trees, killed *annually* since 1927 on the Beaverhead Forest, has shown a remarkable increase. During the year 1927, the number of trees destroyed was well under 1,000,000; by 1930 the number had jumped to over 3,800,000, during the year 1931 more than 12,000,000 trees were killed, and during the season of 1932 over 16,000,000 trees were destroyed. Thus a National Forest that once had an estimated amount of more than 1,270,000,000 board feet of merchantable timber has scarcely a stick of it left.[1]

It is seen, therefore, that the destructiveness of this beetle is great, and where losses may run over $1,000,000 in five years, as

[1] These figures have been secured from unpublished reports of Mr. J. C. Evenden and Mr. A. L. Gibson in the files of the Forest Insect Field Station, Coeur d'Alene, Idaho.

on the Beaverhead Forest, any information that can be secured concerning the beetle and its enemies will be of the greatest value in helping to establish on a sound basis a method of control that will largely prevent losses of such magnitude.

ACKNOWLEDGMENTS

Acknowledgment is made to Dr. F. C. Craighead of the United States Bureau of Entomology for permission to publish much of the material that had been secured by the author while an employee of the Bureau of Entomology; to Mr. J. C. Evenden of the Bureau of Entomology for his kindness in lending reports of the Forest Insect Field Station, Coeur d'Alene, Idaho; and to Mr. W. D. Bedard of the Coeur d'Alene Station for sending me living larvæ of *Coeloides dendroctoni* Cushm. and *Medetera aldrichii* Wh. Without this material none of the morphological work on these species could have been done; to Mr. H. J. Rust of the same station; to Miss Mary Foley of the Bureau of Entomology for drawing and composing Plate XIX, and to Professor O. A. Johannsen, of Cornell University, who gave much aid and advice, and in whose laboratory most of this work was done.

TECHNIQUE FOLLOWED

The morphological studies were made with both living and fixed material. For the external anatomy, living material was generally best. The internal anatomy was studied both by gross dissections and by sectioning. For the gross dissections fixed material was generally used but living material cut open in glycerine was very helpful for the study of the tracheal arrangement. In the study of the muscles, material anesthetized in chloral hydrate and then placed either in formol, or in 70 per cent alcohol gave good results.

Material to be sectioned was fixed either in Carnoy's fixative or in hot Bouin's fixative. The specimens were then run up to 70 per cent ethyl alcohol, then into one-half 70 per cent ethyl alcohol and one-half normal propyl alcohol, and finally after one or two hours, placed in pure normal propyl alcohol for two or three hours more. From here the specimens were placed in clove oil until they sank to the bottom of the vial; next placed

in paraffin for at least four to five hours and then imbedded. Sectioning was usually done at 8 μ. Eosin and Delafield's hematoxylin were used as stains.

The drawings except Plate XIX, were all made by the writer with the aid of either a *camera lucida* or a *camera obscura.*

SYTEMATIC POSITION AND IDENTIFICATION

Coeloides dendroctoni Cushm. belongs to the subfamily Vipiinae. This subfamily was proposed by Gahan (1917) for the Braconinæ of authors when Viereck (1914) showed that *Bracon* F. must be used for the genus *Cremnops* Foerster, belonging to the Agathidinae.

According to Viereck (*l.c.*) Wesmael (1838) proposed the genus *Coeloides* for two species of braconids and Westwood (1840) designated one of them, *initiator* Fabr. as type.

Seventeen species and one variety of *Coeloides* have been described, seven of which are nearctic.

A list of the species occurring in the United States, their author, distribution, and host follow. To the data given by Cushman on the hosts of *C. dendroctoni,* my own records have been added.

Coeloides

brunneri Viereck (1912).
Host: *Dendroctonus pseudotsugae* Hopk.
Locality: Montana.

dendroctoni Cushman (1931).
Hosts: *Dendroctonus monticolæ* Hopk. *Ips oregoni* (Eich.).
Ips emarginatus (Lec.). *Ips vancouveri* Sw.
Orthotomicus cælatus (Eich.).
Localities: Montana, Washington, Oregon.

liopodis Brues (1910).
Hosts: Reared from limb containing *Leiopus alpha* (Say).
Locality: Massachusetts.

pectinator (Say) (1836).
Locality: probably from Northwest Territory.

pissodes (Ashmead) (1888).
Hosts: *Pissodes strobi* (Peck).
Localities: Maine, New Hampshire, Massachusetts, Rhode Island, Connecticut, New York, Pennsylvania.

scolyti Cushman (1931).
Hosts: *Scolytus* spp. *Scolytus ventralis* Lec.
Locality: Washington, California, Oregon.
scolytivorus (Cresson) (1873).
Host: *Scolytus quadrispinosus* Say.
Localities: New York, Missouri.

PREVIOUS STUDIES ON THE MORPHOLOGY OF THE LARVÆ OF BRACONIDÆ

A knowledge of the morphology of the larvæ of a group is of considerable importance in studying its phylogeny and of utmost value for field identification and consequently of distinct economic importance. Unfortunately, few studies have been made on the larvæ of the braconids from a systematic view-point. Many miscellaneous larvæ have been described but to date no one has brought together these descriptions and attempted to work out the characters whereby the subfamilies, at least, could be determined by an examination of the larvæ.

It is beyond the scope of this paper to exhaust the literature on the morphology of the braconid larvae. However, it is believed that the following summary, Table 1, will be of some value in showing the variations of the subfamilies and the need of showing more details in published descriptions so that all the larval structures may be used for purposes of classification. The summary deals chiefly with the number and position of the spiracles for only in the last few years have authors been showing details of the head capsule and internal anatomy in sufficient detail to be of any great value.

The genera in the following summary are placed in the subfamilies according to the classification of Muesebeck (1928).

From the above summary the following key can be made for the subfamilies of the last stage braconid larvæ:

A. Last stage larvæ lacking spiracles ..... Aphidiinæ (*Ephedrus*)
AA. Last stage larvæ with spiracles.
B. Larvæ with nine pairs of spiracles.
C. Larvae with eight ventral abdominal tracheal commissures.
Vipiinæ
Doryctinæ
Hormiinæ ?

TABLE 1

Summary of the position of the spiracles and arrangement of the [illegible]

	Position of Spiracles			Tracheal system Location of Commissures			Authority
	Thor. 1	Thor. 2	Total No.*	Anterior dorsal	Posterior ventral	Ventral abdominal	
Vipiinæ							
Microbracon terebella Wesm.	x	o	9	x	x	x	Salt (1931)
Microbracon brevicornis Wesm.	x	o	9	x	x	x	Genieys (1925)
Cœloides neesi Marshall	x	o	9	x	x	x	Seurat (1899)
Cœloides indagator (Fabr.)	x	o	9		not given		Xambeu (1898)
Doryctinæ							
Doryctes gallicus Rh.	x	o	9	x	x	x	Seurat (l. c.)
Hormiinæ							
Heterospilus cephi Rohw.	x	o	9		not given		Hill & Smith (1931)
Sigalphinæ							
Chelonus annulipes Wesm.	o	x	7	x	o	o	Vance (1932)
Microgasterinæ							
Apanteles thompsoni Lyle	o	x	8	x	o	o	Vance (1931)
Microplitus seurati Marshall	o	x	8	x	o	o	Seurat (l. c.)
Blacinæ							
Eubadizon pallipes Nees	x	o	9		not given		Kojima (1932)
Macrocentrinæ							
Macrocentrus gifuensis Ashm.	o	x	9	x	x	o	Parker (1931)
Opiinæ							
Opius humilis Silv.	o	x	9	x	x	o	Pemberton & Willard (1918)
Diachasma tryoni Cam.	o	x	9	x	x	o	Idem. (1918)
Euphorinæ							
Dinocampus coccinellæ Schr.	o	x	9		not given		Balduf (1926)
Perilitus omophli Lesne	o	x	9		" "		Lesne (1892)
Meteorinæ							
Meteorus nigricollis Thom.	o	x	9	x	o	o	Parker (1931a)
Aphidiinæ							
Aphidius sp.	x	o	9	x	x	o	Seurat (l. c.)
Ephedrus incompletus Prov.	o	o	o	o	o	o	Wheeler (1923)
Alysiinæ							
Dacnusa areolaris Nees	o	x	9	x	x	o	Haviland (1922)
Adelura gahani Baume-Pluvinel	o	x	9		not given		Baume-Pluvinel (1915)

* As the abdominal spiracles, so far as is known, are always in a continuous row beginning with the first abdominal segment, only the total number of spiracles is given as from this data one can easily figure the number of abdominal segments bearing spiracles.

x = presence. o = absence.

CC. Larvæ without ventral abdominal tracheal commissures.
D. Larvæ with a pair of spiracles on first thoracic segment and an anterior dorsal and posterior ventral tracheal commissure.....
Blacinæ
Macrocentrinæ
Aphidiinæ (*Aphidius*)
DD. Larvæ with spiracles on second thoracic segment.
E. Larvæ with only an anterior dorsal tracheal commissure ..... Meteorinæ
EE. Larvæ with both an anterior dorsal and posterior ventral tracheal commissure.
Alysiinæ
Opiinæ
Euphorinæ
BB. Larvæ with eight pairs of spiracles..... Microgasterinæ
BBB. Larvæ with seven pairs of spiracles ..... Sigalphinæ.

DESCRIPTION OF THE STAGES OF COELOIDES DENDROCTONI CUSHM.

Egg

The egg is smooth, pearly white in color and elongate oval in outline. Its average length is about 1.2 mm. It is somewhat larger at one end than the other, and is frequently curved at the smaller end. Its surface is smooth and somewhat shining.

Larva

FIRST STAGE

The first stage larva at hatching is approximately the same size, shape, and color as the egg from which it emerges. It is composed of a head, twelve distinct body segments and an anal knob. The cuticula of the larva bears no setae or other structures that are not found in the full grown larva.

LAST STAGE

EXTERNAL ANATOMY

The full grown larva (Pl. XVII, H) averages from 4 to 6 mm. in length. It is composed of a head and 13 body segments. A pair of spiracles are present on the posterior part of the first thoracic segment and the anterior part of the first eight abdominal segments. The characters of the head capsule can best

be understood by a study of Plate XVII, F. The terminology used for the parts is that of Vance and Smith (1933). The mandibles (Pl. XVII, E) are 0.066 mm. long. Their apex is strongly sclerotized at the margin. Six smaller teeth are present below the main tooth of the mandible a distinct distance from its inner edge.

The metopic suture and tentorial fossae are wanting.

All of the body segments except the last are covered with minute triangular cuticular spines about 0.016 mm. in length. They form a continuous band around each segment. There are, on the average, 106 to 136 spines per square mm. The mid ventral region is not glabrous as described in Genieys (l.c.) and Salt (l.c.) for other Vipiinæ larvæ. Cephalad and caudad at the body sutures the spines gradually thin out so that in the immediate region of the sutures there are no spines. In segments 11 and 12 the spines thin out farther from the sutures so that the bands on these segments are narrower than on the preceding ones. The terminal segment bears six pairs of setæ or setæ-like spines dorsad and four pairs ventrad.

On each of the body segments except the last there are five pairs of larger bristles located as follows: Two pairs dorsal to the spiracles; one pair on the lateral swellings or where these swellings would be if present; one pair below these swellings, and the fifth pair quite on the ventral surface. These bristles are about 0.03 mm. in length and have a distinct circular base.

There is a lateral swelling below each of the spiracles of the abdominal segments.

A prominent inversible pseudopod is present on the dorsum of the first seven abdominal segments. The eighth abdominal segment bears a small hump which is generally visible only in active larvæ. The anterior part of the dorsum of segments two and three each bear a small rudimentary hump.

Internal Anatomy

Tegumentary Muscles of the Body

In the following discussions the origin of the muscles is considered to be at the anterior margin of the segments. Thus, a

ventro-dorsal oblique muscle will extend from the anterior margin of a segment diagonally caudad and dorsad.

The general arrangement of the muscles of the body wall can best be understood by a study of Pl. XVIII, B. The ventral horizontal muscles (vh 1–6) in the thoracic segments tend to coalesce so that in segment 1 the band is usually composed of four muscles and in segment 2, 4 or 5 muscles. All of the ventral horizontal bands of muscles in the abdomen are composed of six muscles except segment 12 where as far as could be determined there are four or five muscles to the band. The muscle arrangement for segment 13 was not worked out but there are only one or two muscles extending into it. The lateral ventro-dorsal oblique muscles (lvdo) often divide to form two separate strands as they extend over the second segment from their insertion. The two strands always reunite before reaching the band of dorso-horizontal muscles.

The muscles forming the dorsal and ventral horizontal bands are the widest of the body muscles. In the middle of the body they are about 0.01–0.008 mm. in width. They narrow posteriorly so that in segment 11 they are from 0.004–0.0058 mm. in width. The total width of the ventral horizontal band in segment 9 in one specimen was 0.058 mm.

DIGESTIVE SYSTEM

The fore-intestine (Pl. XVIII, A) extends back into segment 2 where it unites with the mid-gut. The latter enlarges abruptly and occupies the greater part of the body until it unites with the hind intestine in the posterior region of segment 10. Histologically the epthelium of the mid-gut is composed of large, hexagonal binucleated cells (Pl. XVII, C). The larvæ sectioned were approaching the prepupal stage which may account for the binucleated cells. Unfortunately no larvæ of the earlier stages were available for further investigation. The hind-gut at this point is enlarged and resembles a collar, bearing a ring of papillæ each about 0.007 mm. in length and 0.0028 mm. in width. Though, in one larva 16 papillæ were counted, and in another 12 it seems likely that they are the buds of the adult Malpighian tubules. The papillæ are shown quite a bit larger than they actually are in proportion to the small intestine. The latter

tapers rapidly from the collar until it is about 0.1 mm. in diameter. It unites with the colon, about 0.3 mm. in diameter, at the posterior end of segment 12. The colon tapers gradually, to the anus, forming the rectum in segment 13.

The Malpighian tubules are attached to the small intestine anterior to the collar and extend cephalad as a pair of simple tubes about 0.008 mm. in diameter. They terminate in segment 2. Only traces of silk glands could be found in the larvæ. This may be explained by the fact that the larvæ on which the internal anatomical studies were made had spun their cocoons at least four months or more previously. The glands having performed their function probably atrophied during the time between the completion of the cocoon and the time of sectioning. A large silk press is present in the head.

Respiratory System

All the spiracles on three larvæ were measured. They range in diameter from 0.0288–0.0399 mm. with an average of about 0.0355 mm. The following table, Table 2, will show the variations in size.

Table 2. Diameter of Spiracles of Three Larvæ of *Cœloides dendroctoni* Cushm.

Segment	Larva		Larva		Larva	
	Side		Side		Side	
	Left	Right	Left	Right	Left	Right
1	0.0355	0.0377	0.0399	0.0388	0.0366	0.0355
4	0.0355	0.0355	0.0377	0.0399	0.0366	0.0355
5	0.0333	0.0333	0.0377	0.0377	0.0355	0.0333
6	0.0288	0.0333	0.0388	0.0355	0.0*	0.0355
7	0.0310	0.0333	0.0377	0.0388	0.0333	0.0333
8	0.0310	0.0333	0.0377	0.0366	0.0333	0.0333
9	0.0310	0.0333	0.0388	0.0288	0.0333	0.0333
10	0.0310	0.0333	0.0388	0.0355	0.0333	0.0333
11	0.0333	0.0310	0.0377	0.0355	0.0355	0.0377

* Not measured.

It will be seen from the foregoing table that there is a tendency for the prothoracic spiracle to be the largest.

The shape of the spiracles varies considerably. They are rarely round, generally of irregular outline and frequently appreciably longer than wide.

The cup part of the spiracle is covered over with a layer of cuticle and only a small oval opening in it allows access of air (Pl. XVII, D). The trachea leading from the spiracle to the lateral tracheal trunks is provided with a valve-like structure (Pl. XVII, G, va), the exact nature of which could not be determined. Its position between the base of the spiracle and the longitudinal tracheal trunk varies considerably but it is generally, often considerably, nearer the tracheal trunk than the base of the spiracle.

The tracheal system can best be understood by a study of Plate XVII, B.

Circulatory System

The heart or dorsal vessel (Pl. XVIII, A) originates as the aorta in segment 1 above the œsophagus and behind the brain. It extends abruptly dorsad until it is lying between the two bands of dorsal horizontal muscles in segment 3. In segment 2 it is about 0.036 mm. in diameter. It runs in this position back to segment 12 where it descends slightly towards the colon. As far as could be determined there is a valve near the anterior part of each abdominal segment. None was observed in the aorta. The heart in the abdomen varies in size. In segment 4 it was 0.05 mm. in diameter.

Adipose Tissue and Urate Cells

The fat-bodies (Pl. XVII, A) fill almost all the cavities of the larva, around the internal organs, from segment 1 to 12 inclusive. No segmental arrangement was present. They are composed of rather compact masses of irregular layers. Scattered among the fat bodies from segments 4 to 12 inclusive are numerous yellowish-white bodies, the urate cells (Pl. XVII, A). These are most abundant on the sides of the larva, fewer are present dorsad and none ventrad.

These bodies are quite obvious, especially in the full grown larvæ; none was observed in the first stage larvæ. In field work one can easily distinguish the larvæ of *Cœloides* from chalcid larvæ by the presence of these cells. The chalcid larvæ observed lack any cells that stand out so prominently as the urate cells of *Cœloides*. Prominent urate cells have been observed in other braconid larvae not parasitic on barkbeetles.

Nervous System

The nervous system (Pl. XVIII, A) consists of a bilobed brain (located in the anterior part of segment 1, and the posterior part of the head), a subœsophageal ganglion, and eleven segmental ganglia. The ganglia are connected to each other by paired connectives. The terminal ganglion is larger than the others indicating a coalescing of the ganglion of segments 12 and 13 with that of the proceding ganglion. From each of the ganglia a pair of main nerves runs laterad between the body wall and the integumentary muscles as far as the spiracles. Beyond this point they could not be traced.

Pupa

The female pupæ range from 4.0–5.5 mm. in length and 1.4–1.8 mm. in width.

The caudal extremity of the wing pad extends to slightly beyond an imaginary line drawn half way between the apex of the head and the caudal extremity of the last ventral sternum. The end of the pad is slightly anterior to the mid-part of the third visible abdominal segment (viewed ventrad). The prothoracic legs extend to slightly less than two-thirds the length of the wing pads, the mesothoracic legs extend a slight distance beyond the end of the wing pads, *i.e.*, to a point slightly anterior to the posterior margin of the third visible segment. The metathoracic legs extend almost to the extremity of the last visible abdominal segment, and the antennæ end at a point slightly short of the tip of the metathoracic legs. The ovipositor curves backward over the abdomen and ends at a point midway in the second visible abdominal segment (viewed dorsad). The last larval skin is always found adhering to and covering a good portion of the ovipositor.

There is considerable variation in the specimens examined. In some cases the wing pads extend to the caudal extremity of the third abdominal segment; the prothoracic legs extend fully two-thirds the length of the wing pads; the mesothoracic legs reach beyond the anterior margin of the fourth visible abdominal segment, the antennæ end even with, or extend slightly beyond the extremities of the metathoracic legs, and the extremity of the ovipositor attains the anterior margin of the first visible abdominal segment.

Urate cells are visible through the cuticle but are less numerous than in the full grown larva.

Cocoon

The cocoons range from 4 to 8 mm. in length. They are slightly circular in cross section and oval in shape. They vary in color from tan or dark brown to nearly white.

Adult

The following is copied from the original description by Cushman (*l.c.*).

"*Female.*—Length 4 mm. or less. Head nearly as broad behind eyes as at eyes, the temples strongly convex, the width from front to back about equal to that of eye; the so-called "mouth opening" much narrower than its distance from the eye and about as broad as length of malar space; malar space about half as long as eye; face minutely punctate; clypeal groove distinct medially; antennae slender, third joint of flagellum hardly concave below, very nearly as long as fourth, the latter fully twice as long as thick. Thorax weakly depressed, polished and virtually unsculptured throughout, only the metapleurum sparsely punctate; scutellar fovea minutely foveolate; stigma broad, radius slightly before middle; second cubital cell long, the second abscissa of radius much longer than first intercubitus and parallel with second abscissa of cubitus. First tergite much longer than broad, finely rugulose, the lateral furrows foveolate, the median area about three times as broad as the lateral rims; second tergite shorter than third, more or less emarginate in apical middle, more or less rugose medially and with a more or less distinct raised area in basal middle; sheath about three-fourths as long as body (relatively longer in small specimens).

"Head black, orbits, cheeks, malar space, mandibles, and clypeus testaceous; labium, maxillæ, palpi, and antennæ black; thorax and legs black, trochanters and apices of front femur and tibia more or less reddish, postscutellum and a median streak on propodeum also more or less reddish; abdomen usually testaceous with only the first tergite black, in small specimens more or less blackish with tergites 2 and 3 pale or largely brownish black.

"*Male.*—Essentially like female, but more frequently with abdomen largely blackish and often with apex and lateral areas of scutellum stramineous.

"*Type-locality.*—Sula, Montana.

"*Type.*—Cat. No. 43,635, U.S.N.M.

"*Hosts.*—*Dendroctonus monticolæ* Hopk.; *Ips oregoni* (Eich.)."

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Explanation of Symbols Used in the Illustrations

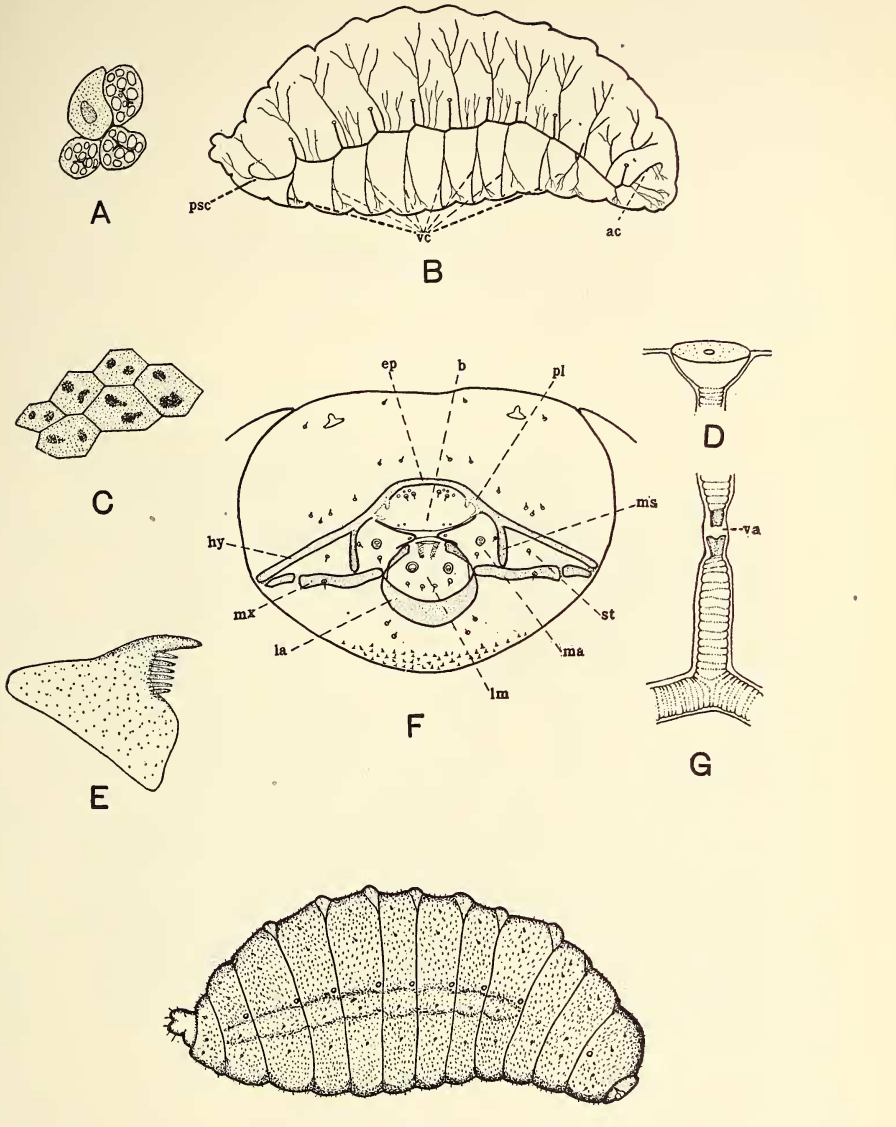
ac, anterior dorsal commissure.
b, labrum.
ddvo, dorsal dorsoventral oblique muscle.
dh_{1-5}, dorsal horizontal band of muscles.
ep, epistoma.
hy, hypostoma.
is, vertical intersegmental muscle.
la, labiostipital sclerome.
ldvo, lateral dorsoventral muscles.
lm, Labiostipites.
lvdo, lateral ventrodorsal muscles.
ma, maxillary stipes.
ms, stipital sclerome.
mx, maxillary sclerome.
pl, pleurostoma.
psc, posterior ventral commissure.
se, vertical segmental muscle.
sh, horizontal segmental muscle.
sp, spiracle.
st, cardo.
va, tracheal "valve."
vc, ventral abdominal commissures.
vh_{1-6}, ventral horizontal band of muscles.

PLATE XVII

Coeloides dendroctoni Cushm.

Final Instar Larva

A. 3 fat cells and 1 urate cell.
B. Tracheal system.
C. Epithelium of mid-intestine.
D. Spiracle.
E. Mandible.
F. Head capsule.
G. Portion of trachea connecting main longitudinal trunk with spiracle.
H. Larva.



COELOIDES DENDROCTONI

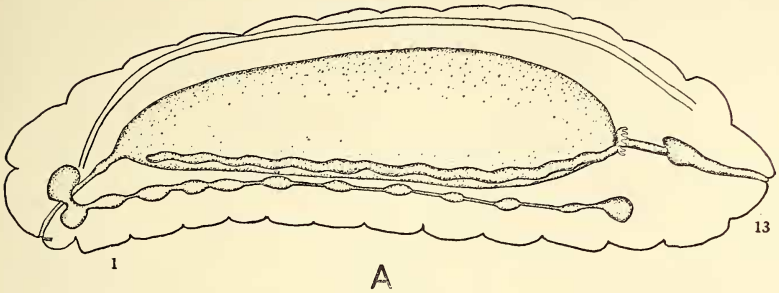
PLATE XVIII

Coeloides dendroctoni Cushm.

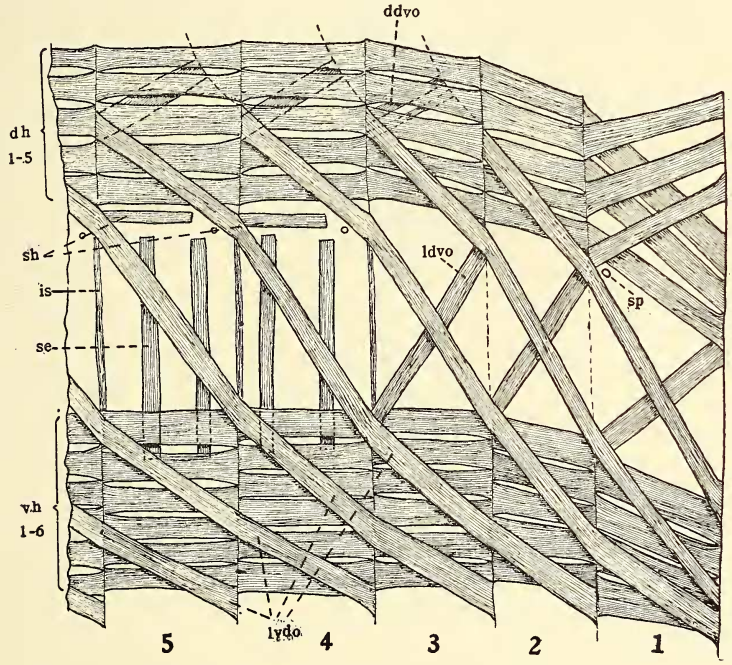
Final Instar Larva

A. Lateral view showing position of main nervous system, digestive tract, Malpighian tubes, and heart.

B. Lateral view of segments 1 to 5 inclusive showing muscle system.



A



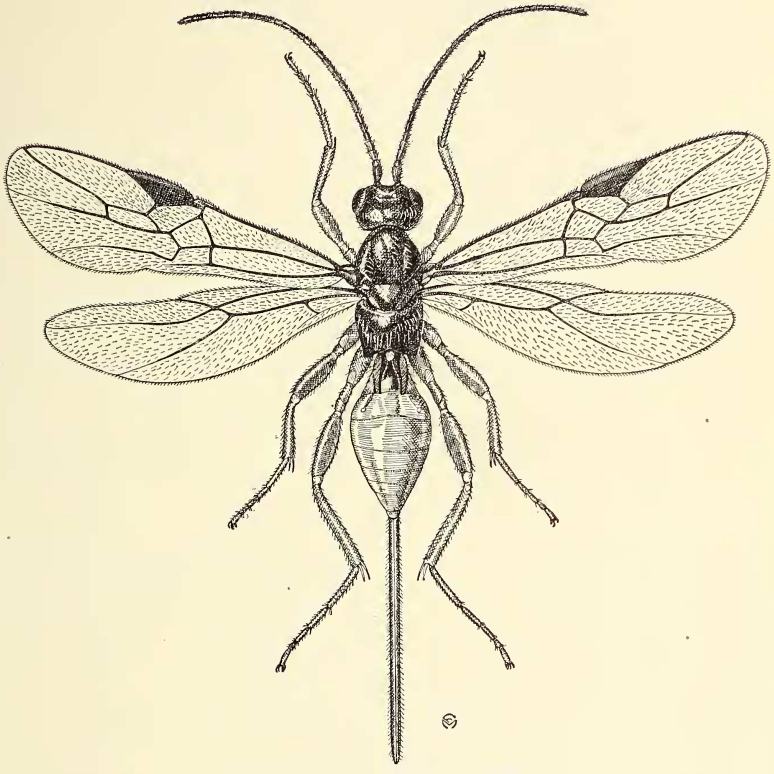
B

COELOIDES DENDROCTONI

PLATE XIX

Coeloides dendroctoni Cushm.

Female.



COELOIDES DENDROCTONI